ON THE BUTTERFLIES' TRAIL

By HERMANN HÖNE

When in the summer of 1942 we asked our readers to give us their opinion on all the articles published by this magazine until then, Dr. Höne's "The Butterflies Told Me" (March 1942) turned out to have been one of the favorites. Here, in a new article, Dr. Höne answers the question as to the origin of butterflies, basing his theory on discoveries made by him in fifty years of scientific work, largely in cooperation with Prince A. Caradja, and on his own collection of almost a million Eastern Asiatic lepidoptera.

A wealthy butterfly collector who had concentrated on European butterflies decided one day to add overseas specimens to his collection. As he had plenty of time and money, he made up his mind not to do so by means of purchase or exchange but to catch all the specimens himself and in this way to inform himself of their life and habits.

For days he studied his atlas; and as he only wished to catch lepidoptera of the palearctic zone, i.e., the region which covers all of Europe, the northern part of Africa up to the Sahara, and the major part of Asia up to the Himalayas, including Siberia, northern and central China, as well as Japan, he finally decided to travel to Shanghai. After all, everything was so different in China from Europe, even the people, and Shanghai was some 5,000 miles away from Germany. It seemed obvious that plants and creatures must all be different, too, from those to be found at home.

The day after his arrival in Shanghai, he set off with his net and collecting box, choosing Hungjao as his destination. As soon as he had crossed the railway, he began his hunt. The first butterfly he saw was a *Pieris*. In a moment he had it in his net. And now let us listen to what he has to say as he mutters to himself while hunting:

"Well, well, isn't that our cabbage butterfly (*Pieris rapae*) from home? Strange, lying like this on my palm I can't make out any difference off hand from those in Germany. . . . But what is that? It looks just like our golden eight (*Colias hyale*), a male, a beautiful dark-yellow one; looks to me slightly bigger than those at home, but otherwise it is exactly the same. Indeed, here is the clearly marked 8 on the lower wings. . . . Good Lord, isn't that a Chrysophanus over there? I can hardly believe it: *Chrysophanus phlaeas*, exactly the same one we have back home. Am I dreaming? I thought I was in China! . . . . Oh, what was that reddish-brown shadow fluttering past? Where did it go off to? Over there, it settled on the grave mound, yes, it is hanging on a small yellow chrysanthemum blossom. And what is it? A *Vanessa*! That beats everything, it is our golden C (*Polygonia c-aureum*).

"Is this just a coincidence? No, I am sure I'll find something special. Let's get off this field. Over there on the road is a fine old poplar, let's see what I can find on the bark, perhaps something new in the way of moths . . . . There, an empty old cocoon, looks to me like our pussmoth (*Dicranuria vinula*), yes, and right next to it a new, just completed cocoon, and there—believe it or not—comes a caterpillar creeping down the trunk, already colored red, ready to spin a cocoon. There can be no doubt, it must be the same pussmoth as at home. In four weeks I'll search the poplar and willow trunks for cocoons, then I'll have some nice fresh specimens in spring. . . . Ah, the first geometrid in China, five steps away there on the telegraph pole! Now don't tell me that this is *Boarmia selenaria*, the same one you can find everywhere in Europe. But it is, there can be no denial."

And so the collector went on, finding one butterfly after another practically identical with those he had known at home, whether it was a painted lady, a red admiral, a convolvulus hawk moth, a swallowtail. Finally, when he was ready to go back to the city, a brimstone butterfly came flying past, another old friend from Germany. As he added it to his day's collection, he thought:

"If there isn't a radical change in my catches in the next few days, what am I to show my collector friends at home? If I show them today's bag, nicely displayed in a box, and tell them that these are all butterflies I caught one fine morning near Shanghai in China, they will laugh at me and say, 'No, my boy, you needn't think we're as stupid as all that. You can't fool us: you've caught all these specimens in the fields outside our town. Why, perhaps you've never been to China at all!'"

So the butterfly collector remained in Shanghai for another six months and, although he managed in time to catch some specimens which differed from those in his own country, he found on the whole that the butterfly world

of the environments of Shanghai was practically identical with that of Germany. In time he discovered that the Shanghai butterflies bore different names from those in Germany which they resembled so greatly. Practically all of them had been described by scientists as forms of the species native to Europe: quite a natural trend in nomenclature, for butterflies were first studied and described in Europe, and it was only many years later that the creatures of the Far East were included in these studies. The natural development, origin, and migration of these lepidoptera, however, has gone exactly the opposite way. It is here in China, on the former continent of Angara, that the butterflies came into existence and migrated during the Tertiary to Europe, so that out here in the East we find the original species while in Europe those we meet with are migrated and modified forms and species. So the original home of the lepidoptera in Europe is Eastern Asia and not Europe, as was maintained and generally believed until recently.

BEFORE THE ICE AGE

On what grounds do we support our claim that the preglacial European fauna originated in Asia?

(1) There is no European form which, in its habitus, does not fit into the framework of a common Eurasian fauna.

(2) The outstanding characteristic of the entire preglacial European fauna seems to have been a pronounced uniformity. There was at that time probably no reason for any strong differentiation, as the climate in Europe as well as in Asia was quite uniform, viz., it was milder than now and in parts probably rainier, almost subtropical.

(3) In the case of many butterflies, it can be proved that the most primitive forms and species are to be found at present only in Eastern Asia, the next most primitive also there but in part also in Central Asia and North America as well as in a modified form in the entire eremic (from Greek *eremia*=desert) subregion of the palearctic region. The apparently most highly developed forms, on the other hand, are to be found chiefly in Europe where, under the influence of later events, they underwent a considerable evolution and split up into numerous races and forms.

(4) Among these highly developed Western forms, however, many relics of the preglacial Eurasian fauna maintained themselves in Europe, too. It is these very relics which almost force one to assume an originally common fauna and a mild warm climate in Europe. As regards the nature of these relics, it is well known that in the course of evolution certain forms and groups proved extremely rigid, remaining unchanged through entire geological ages, while others reacted astonishingly quickly, even explosively, to factors of environment. Such rigid forms, which can only be regarded as preglacial relics, have survived at certain places up to the present day and are for us, so to speak, living fossils from which we can deduce facts about their time of origin.

The assumption of an exclusively Asiatic origin of the preglacial European fauna has, however, been contested, the most notable objections being the following:

(1) For the Western expansion of the Asiatic fauna it was, of course, necessary that a continuous land connection without obstacles existed between Europe and Eastern Asia. It has been claimed that the channel connecting the Sea of Tethys east of the Urals with the Polar Seas in the pre-Oligocene period prevented a migration of Asiatic elements to the west. Detailed studies made on the spot, however, have proved that this dividing channel had ceased to exist toward the end of the Tertiary as a result of the raising of Central Asia.

(2) Until recently fossil discoveries had led to the general assumption that many creatures must have migrated to Europe from North America via a land connection, the "Icelandic Bridge," which allegedly existed up to the Pleistocene. Detailed comparisons of the lepidoptera of Europe and North America have, however, resulted in the conclusion that there can never have been such a land connection. Apart from a few circumpolar faunal elements, Europe has only very few species in common with North America which do not also occur in Eastern Asia. There is far less similarity on both sides of the Atlantic than between Eastern Asia and Western Europe or between the faunas of Eastern Asia and North America. This fact, based on statistical lists, is easily explained by assuming an Asiatic origin of most creatures for North America as well as for Europe.

(3) As for the erroneous assumption of an indigenous European fauna, the proof we shall bring in the following that the European fauna originated without exception in Asia is enough to exclude this possibility.

THE GLACIAL EPOCH

There was, we said, in the whole of Eurasia a preglacial fauna which in its uniformity, and living in a mild, warm climate, formed a well-balanced, harmonious great biocoenose, which appeared to be developing along quiet, normal lines. This quiet evolution was, however, disrupted by a mighty natural phenomenon which brought utter confusion into the European fauna, even threatening its existence, but on the other hand also forcing it to offer utmost resistance and driving it into entirely new evolutionary trends: the ice age came.

In Europe the polar ice masses advanced periodically toward the south and covered almost half of the land formerly free of ice with one continuous blanket of ice, while tre-

mendous glaciers flowed down from the Alps in the opposite direction. But in between there remained in Central Europe certain tracts and countless small enclaves free of ice; they formed refuges for the more resistant types of butterflies, offering them a chance to survive the critical times. Even in the Alps some preglacial European faunal elements were able to survive in similar refuges where, adapting themselves to the mountain climate, they have maintained themselves to this day.

The result of these glacial invasions was a profound change in the Central European lepidoptera fauna. Since, however, the glaciers were a phenomenon limited in extent and time, they did not succeed in Central Europe in destroying the entire original fauna; but they did affect it deeply by bringing about profound changes in the biotopes within their range.

But in part the old fauna was able to take refuge in those corners of Europe which had remained free of ice, where it could survive more or less in entirety. This happened, for instance, in the southwestern parts of the Urals down to the Caspian and Black Seas, in some parts of the Alps, and of the eastern Pyrenees; then in the Atlantic coastal zone, but above all the region of the southwestern peninsulas and islands (Italy, Sicily, Corsica, Spain) down to northwest Africa.

The fate of the boreal (i.e., northern) Eurasian fauna of Europe was still more significant. The northern lepidoptera species, which until then had eked out a meager existence in Lapland, Kola, and in northeastern Europe and the northwestern corner of Asia, fled southward before the advancing inland ice and in this way arrived as foreigners in lower latitudes. Here they forced out and in places supplanted those forms accustomed to a mild, warm climate. With the return of normal conditions, the majority of the polar species withdrew to the north again; another part found suitable homes in the mountain regions of Central Europe; and others again adapted themselves to the changed environment and intermingled with the newly advancing thermophile elements, i.e., elements dependent on a warm climate. Thus a mixed fauna came into being at that time already in Central Europe, including, in addition to the original Eurasian forms now predominant in the south, numerous preglacial polar forms.

Similar events and changes, only on a larger scale, also took place in western Central Asia. In southern Siberia as well as in Transcaucasia, Palestine, Fergana, Bokhara, and elsewhere, there were numerous extensive refuges for the fleeing preglacial fauna and flora, as can be proved by the present composition of the fauna. In the eastern parts of the Asiatic continent and in Japan, where there was no pronounced glacial period, the lepidoptera found particularly favorable conditions. This enabled them to pass through a comparatively recent time of flourishing, which explains the wealth of forms in these parts. Now we also understand why the lepidoptera fauna of these regions, which were spared acute changes in climate, has differentiated itself less sharply than in Europe, and why the species and genera have in many cases retained their original archaic character up to the present.

For similar reasons as in Eastern Asia, the old preglacial fauna of southwestern Europe and northwest Africa survived in its most original form, so that at present it is those countries of Eurasia which are furthest removed from each other that show the greatest affinity in their faunas. Even the comparatively recent desiccation of the climate in Spain and all of North Africa has only caused a corresponding modification of forms but no essential change in the fauna as a whole.

AFTER THE GLACIAL EPOCH

As we have seen, the main—and for our understanding of evolution most important—effect of the ice age was the disruption and disintegration of the European (and Western Asiatic) lepidoptera fauna; connected with this was a localization of the various groups of elements that had arisen.

This dislocation and isolation was bound to produce various effects under the dominating influence of the changes in climate. At first a severe selection of species took place, based on their innate power of resistance. The weaker species disappeared. Another result, however, was the splitting up of species into varieties, local races, and mutants. Finally, the change in the manner of living enforced by outward factors also resulted in a biological, temporal, or somatic estrangement of species, which is indicated particularly by the interesting "double species" discovered in growing numbers in recent times; in other words, new species arose.

Among the various large and small biocoenoses which were now separated in space, a sharp differentiation also occurred. Each of them subsequently altered independently in various divergent directions, corresponding to the nature and peculiarities of the biotope into which it had happened to get. As early as toward the end of the glacial period, several such sharply differentiated regional and local faunas seemed to have developed; for some of these, the following names have become generally accepted: boreal, alpine, Baltic, Atlantic, Lusitanian, Mediterranean, southern Russian, Pontic, eremic, etc.

In Europe, such strongly differentiated regional and local faunas developed chiefly in those refuges into which the native preglacial fauna had withdrawn during the ice age; it is there, too, probably that all subspecies developed as well as all those forms which we now explain as endemic. Therefore, the basis of

these regional faunas is still formed by the old Eurasian fauna. Of course, not all species differentiated themselves equally sharply: many, probably even the majority, simply went on developing in an entirely normal manner.

After the ice age and the advent of more favorable climatic conditions in Central and Northern Europe, the original fauna, which had been temporarily forced into the refuges and into southern regions, endeavored to spread anew in the direction indicated by the changed environment; it had to fill up the faunal gaps left by the withdrawal of the glaciers. Hence Central and Northern Europe were at first probably repopulated exclusively by the old Eurasian species indigenous to those regions before the ice age, although they were now more or less modified in many cases. The new advance of Mediterranean elements, i.e., originally also native Eurasian species, to Central Europe is particularly interesting: since the Alps formed an insurmountable barrier, this migration could only move along a few routes which can still be traced.

The repopulation of Central and Northern Europe was given a special note by the fact that a number of boreal species—which had formerly not been present there—had remained behind after the glacial period. Wherever the advancing old fauna met with these boreal elements, the result was a mixed fauna which can also still be traced.

NEW IMMIGRATION

At the same time, the constant improvement in the climate of Europe also made possible a new, postglacial expansion of Asiatic faunal elements toward the west and into Europe. The strongest postglacial migration into Europe took place from Siberia. On the whole, these new additions consisted merely of the same species which had already migrated to Europe before the ice age. This postglacial flow from Siberia filled up the original Eurasian fauna of Europe again, as far as some species had been destroyed by the glaciation; its main effect, however, was that when the younger, more resistant forms of this migration met with the older forms as they had been modified in Europe, the former prevailed, the result being a far-reaching uniformity in the Siberian types of today. This uniformity has led to a "Siberian fauna" being spoken of, but it must always be emphasized that this "Siberian fauna" is in reality only part of the old, preglacial Eurasian fauna. The duality of its occurrence in Europe and Siberia must not lead to the erroneous idea that we are confronted here by any new faunal elements which did not immigrate until after the glacial period.

Let us recall here that the postglacial Siberian migration was limited to Northern and Central Europe, and that it never reached the southern regions (e.g., Transcaucasia, the Balkans, Sicily, southern Spain, North Africa, etc.); in all modified regional faunas, refuges, enclaves, etc., especially in the Mediterranean and eremic faunas, we hence find relics, i.e., more or less modified descendants of the original Eurasian fauna, even though the same species may since have developed along different lines in Central Europe and Siberia.

In addition, there have been several other migrations into Europe since the ice age. The warm, dry climate of the last interglacial period favored the advance of Western Asiatic steppe forms into Europe, so that such isolated forms occur in Transylvania, Hungary, and even Thuringia. Then the change east of the Carpathians to a warm, damp climate with mild winters after the last glacial period enabled various thermophile species to penetrate to the Baltic coast, where they can still be found side by side with numerous glacial relics. Not long after, however, the climate east of the Carpathians turned warm and dry, becoming typically continental. This immediately caused an invasion of southern Russian steppe species up to a line which follows the Carpathians. This faunal migration is still continuing, particularly in Rumania.

* * *

To sum up, we have arrived at two basic conclusions resulting from the observations described above:

(1) Before the ice age, the whole of palearctic Eurasia was populated by a uniform fauna. This basic uniformity has survived to this day, in spite of profound regional changes and in spite of the present disjunctive occurrence of certain species and the resulting formation of subspecies and particular endemic forms. All existing differences can be traced to the effect of never-resting evolution. The assumption of an indigenous fauna of any one region, especially of Europe, cannot be substantiated.

(2) The center of origin of this fauna is to be sought in Eastern Asia, probably in the old Angara continent of the geologists, whence it expanded radially to Europe as well as North America, Southern Asia, and Malaysia. No single instance of a postglacial expansion in the opposite direction, particularly from Europe to Asia, has been established.

Success

At the start of what was hopefully called Juvenile Delinquency Prevention Week, a detective-sergeant was shot and killed in Montreal, a 17-year-old and a 15-year-old were arrested and charged with the murder. In the roundup of suspects, police grabbed 150 other youths, obtained confessions to 50 other crimes.